Biological Conservation 174 (2014) 93–100

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Modeling effects of conservation grassland losses on amphibian habitat

David M. Mushet *, Jordan L. Neau, Ned H. Euliss Jr.

U.S. Geological Survey, Northern Prairie Wildlife Research Center, 8711 37th Street SE, Jamestown, ND 58401, USA

ARTICLE INFO

Article history:
Received 14 November 2013
Received in revised form 24 March 2014
Accepted 1 April 2014

Keywords:
Amphibians
Conservation Reserve Program (CRP)
Grassland conservation
Habitat modeling
InVEST
Land-use change
Prairie Pothole Region

ABSTRACT

Amphibians provide many ecosystem services valued by society. However, populations have declined globally with most declines linked to habitat change. Wetlands and surrounding terrestrial grasslands form habitat for amphibians in the North American Prairie Pothole Region (PPR). Wetland drainage and grassland conversion have destroyed or degraded much amphibian habitat in the PPR. However, conservation grasslands can provide alternate habitat. In the United States, the Conservation Reserve Program (CRP) is the largest program maintaining grasslands on agricultural lands. We used an ecosystem services model (InVEST) parameterized for the PPR to quantify amphibian habitat over a six-year period (2007–2012). We then quantified changes in availability of amphibian habitat under various land-cover scenarios representing incremental losses (10%, 25%, 50%, 75%, and 100%) of CRP grasslands from 2012 levels. The area of optimal amphibian habitat in the four PPR ecoregions modeled (i.e., Northern Glaciated Plains, Northwestern Glaciated Plains, Lake Agassiz Plain, Des Moines Lobe) declined by approximately 22%, from 3.8 million ha in 2007 to 2.9 million ha in 2012. These losses were driven by the conversion of CRP grasslands to croplands, primarily for corn and soybean production. Our modeling identified an additional 0.8 million ha (26%) of optimal amphibian habitat that would be lost if remaining CRP lands are returned to crop production. An economic climate favoring commodity production over conservation has resulted in substantial losses of amphibian habitat across the PPR that will likely continue into the future. Other regions of the world face similar challenges to maintaining amphibian habitats.

Published by Elsevier Ltd.

1. Introduction

Amphibians perform a variety of supporting, provisioning, regulating, and cultural services valued by society as defined by the Millenium Ecosystem Assessment (2003). Within aquatic ecosystems, amphibians affect algal communities, invertebrate populations, predator dynamics, and nutrient cycling (Seale, 1980; Vanni, 2002; Davic and Welsh, 2004). Their ectothermic physiology provides for the efficient transfer of ingested energy to other trophic levels of an ecosystem (Pough, 1980). As larval amphibians metamorphose to adults and leave aquatic habitats, they move nutrients from aquatic to terrestrial ecosystems (Regester et al., 2006). In addition to being critical components of important ecosystems (Lannoo, 2012), amphibians provide additional benefits through their use in scientific research and teaching (O'Rourke, 2007). Cultural services (Millenium Ecosystem Assessment, 2003) also arise from the diversity of shapes, colors, and rich vocalizations of amphibians (Cox et al., 2008). Preserving amphibian biodiversity has many positive benefits to society, some of which relate simply to morals and values.

Despite the societal benefits of maintaining amphibians, they are disappearing from global ecosystems at a rate estimated to be over 200 times greater than the background amphibian extinction rate (McCallum, 2007). Within the United States, amphibian occupancy of ponds and comparable habitats declined 3.7% annually from 2002 to 2011 (Adams et al., 2013). With approximately one third of all amphibian species being listed as globally threatened and over 43% experiencing population declines (Stuart et al., 2004), amphibians as a group are far more threatened than either birds or mammals (Stuart et al., 2004) and have extinction rates exceeding those of all other vertebrates (Regan et al., 2001). While the potential causes of amphibian declines are diverse and include important issues such as the spread of chytrid fungus, the major contributing factor to amphibian declines globally is habitat destruction and/or degradation, affecting an estimated 63% of all amphibian species (Chanson et al., 2008).

Many amphibians are biphasic in that they rely on both aquatic and terrestrial habitats to complete their life cycle (Harper et al., 2008). In the Prairie Pothole Region (PPR) of North America, the need for aquatic habitats for breeding and subsequent larval development is typically met through the use and availability of palustrine wetlands (Mushet et al., 2012a). After metamorphosis, adults use surrounding grassland habitats for foraging, cover, and

* Corresponding author. Tel.: +1 701 253 5558; fax: +1 701 253 5553.
E-mail address: dmushet@usgs.gov (D.M. Mushet).

http://dx.doi.org/10.1016/j.biocon.2014.04.001
0006-3207/Published by Elsevier Ltd.

overwintering (Semlitsch, 2000; Mushet et al., 2012a), a notable exception being the northern leopard frog (*Lithobates pipiens*), which returns to aquatic habitats for overwintering (Merrell, 1970). Thus, habitat for PPR amphibians is composed of both wetland habitats and surrounding areas of terrestrial habitat (Semlitsch and Bodie, 2003).

To offset the loss of native habitats and the services they provide, both governmental and nongovernmental organizations have made significant monetary investments in the PPR to restore and protect both grassland and wetland habitats. Given the prominence of agriculture throughout the PPR, the most wide reaching conservation efforts have been associated with various programs of the U.S. Department of Agriculture (USDA). Within the USDA, the Conservation Reserve Program (CRP) has had the largest impact in terms of total area affected (Table 1; USDA, 2013). Like many other conservation programs, CRP is a voluntary program that provides producers with a monetary incentive to establish and maintain perennial cover on upland areas enrolled in the program. In the PPR, this perennial cover is typically grass species intermixed with various forbs, especially legumes. When combined with extant natural or restored wetlands, these CRP grassland habitats may mitigate habitat losses associated with agricultural production. However, payments to farmers participating in conservation programs have failed to keep pace with rising values of agricultural commodities and profits that can be realized through their production (Rashford, 2011). In addition, warmer growing season temperatures, recent increases in summer precipitation, and availability of new varieties of pesticide tolerant and drought resistant crops has facilitated the production of higher valued row crops (e.g., corn and soy beans) in areas previously dominated by small grain production. The disparity of profits that can be realized through participation in a conservation program versus the production of agricultural commodities has resulted in a recent exodus of PPR farmers from conservation programs. This exodus has resulted in the return of vast tracts of grasslands created through these programs to agricultural production, primarily row crops (Euliss et al. 2010; Classen et al. 2011; Rashford et al. 2011). With CRP contracts on significant amounts of land expiring in the next five years and high commodity prices likely to continue, loss of additional conservation grasslands to crop production will most likely occur (Wright and Wimberly, 2013).

The objectives of our research were: (1) to quantify amphibian habitat within the U.S. portion of the PPR over a time period in which a significant amount of conservation grasslands were returned to crop production and (2) to investigate how continued losses of these grassland habitats might affect the availability of habitat needed by amphibians. In previous work, we developed a conceptual model depicting relationships among amphibians and specific components of the PPR landscape important for maintaining amphibians (Mushet et al., 2012a). We also performed habitat suitability mapping to further identify species-specific habitat components used by amphibians (Mushet et al., 2012b). Here we incorporate knowledge gained through these and other amphibian focused research efforts (e.g., Balas et al., 2012) into an ecosystem services modeling framework.

2. Material and methods

2.1. Study area

The PPR covers approximately 820,000 km^2 of the United States and Canada (Fig. 1). Glacial processes shaped the region and created a landscape consisting of innumerable palustrine wetlands (often termed prairie potholes) scattered within a grassland matrix (Kantrud et al., 1989). This intermixed grassland and wetland landscape provides habitat for a wide variety of flora and fauna including grassland and wetland plants (NGPFAP, 2001), waterfowl (Batt et al., 1989), other wetland dependent birds (Igl and Johnson, 1998), grassland birds (Swengel and Swengel, 1998), small mammals (Fritzell, 1989), aquatic and terrestrial invertebrates (Swengel and Swengel, 1998; Euliss et al., 1999), and amphibians (Larson et al., 1998). In addition to supporting grassland and wetland dependent biota, the combination of the region's rich glacial soils and its temperate climate has made it an ideal area for agricultural commodity production (Leitch, 1989). To facilitate agricultural production since European settlement, approximately 95% of native tall-grass prairie and 60% of native mixed-grass prairie in the PPR have been converted to croplands (Higgins et al., 2002). Additionally, 35–89% of the wetlands in portions of the United States PPR (Dahl, 1990) and 71% in the Canadian PPR (Environment Canada, 1986) have been drained. In an effort to increase our understanding of how landcover change affects the availability of amphibian habitat, we quantified this habitat across the three Level III ecoregions (Northern Glaciated Plains, Northwestern Glaciated Plains, and Lake Agassiz Plain; USEPA, 2013) and one level IV ecoregion (Des Moines Lobe, USEPA, 2013) that constitute the United States portion of the PPR (Fig. 1).

2.2. Modeling approach

We used the Biodiversity Module of the Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST) modeling suite version 2.4.5 (Natural Capital Project, 2013) to quantify amphibian habitat. InVEST is a suite of spatially based modeling tools used to quantify a variety of services derived from ecosystems, including the maintenance of biodiversity. The Biodiversity Module of InVEST uses habitat quality as a surrogate for biodiversity (Nelson et al., 2011). Using InVEST, we modeled amphibian habitat over a period of declining CRP enrollments (2007–2012) and made future projections under various scenarios of continued loss of CRP grasslands varying from 0% loss up to a complete (i.e., 100%) loss of CRP grasslands from the PPR landscape.

We created land-cover data layers for 2007–2012 by combining National Agricultural Statistics Service (NASS) cropland data layers for each year with rasterized National Wetland Inventory (NWI) data. Areas enrolled in CRP were uniquely identified using a shape file data layer obtained from USDA Farm Service Agency's Economics and Policy Analysis Staff. We defined amphibian habitat as being palustrine wetlands plus a surrounding terrestrial buffer extending 160-m beyond the wetland edge. If all or portions of a buffer were in a cropland or another developed (e.g., urban) cover

Table 1
Area (ha) of land within Minnesota (MN), North Dakota (ND), South Dakota (SD), and Iowa (IA) enrolled in the U.S. Department of Agriculture's Conservation Reserve Program, 2007–2012 (USDA, 2013).

State	2007	2008	2009	2010	2011	2012	Change 2007–2012	% Change 2007–2012
MN	740,918	718,466	686,395	666,479	634,496	568,693	−172,295	−23
ND	1,372,332	1,205,433	1,155,257	1,076,375	969,053	730,595	−641,737	−47
SD	631,534	527,196	505,804	467,274	446,761	396,895	−234,639	−37
IA	798,047	732,827	690,092	680,700	671,500	620,078	−177,969	−22
Total	3,542,831	3,183,992	3,037,548	2,890,827	2,721,809	2,316,191	−1,226,640	−35

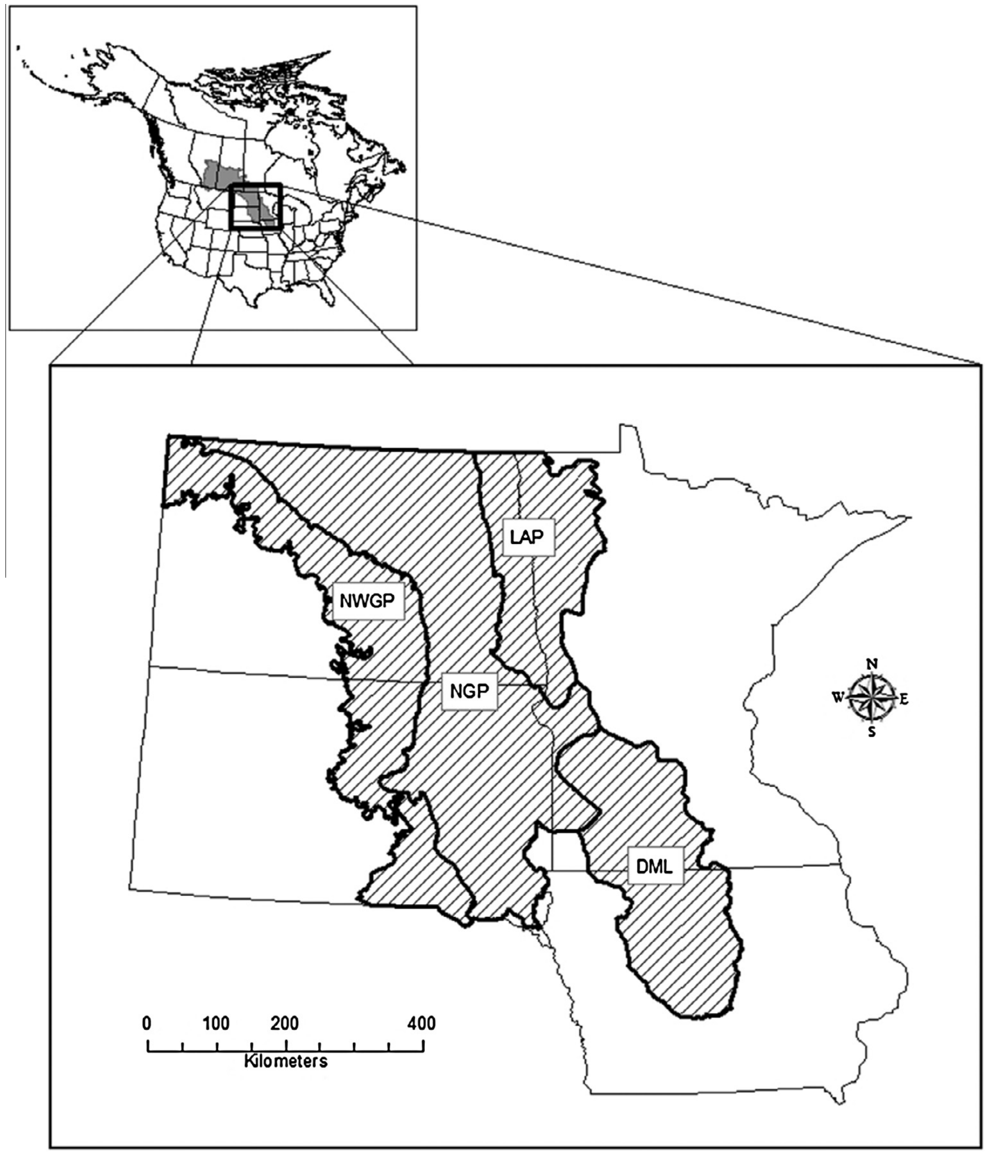

Fig. 1. Map of the Prairie Pothole Region of North America (shaded area) and the Northern Glaciated Plains (NGP), Northwestern Glaciated Plains (NWGP), Lake Agassiz Plain (LAP), and Des Moines Lobe (DML) ecoregions (USEPA, 2013) of the United States (enlargement).

type, those portions were not included in the habitat designation. Our 160-m terrestrial buffer width was selected to approximate the 159-m wide area surrounding wetlands that Semlitsch and Bodie (2003) identified as habitat for wetland breeding amphibians. Thus, while many species use terrestrial habitats farther than 160-m from a wetland edge, all use the area between the wetland edge and the outer limit of our 160-m buffer.

For our CRP grassland loss scenarios, we used the 2012 land-cover layer described above to represent current land-cover. We assigned a random number drawn from an even distribution (0.0000–1.0000) to each CRP field within the PPR. We then converted a scenario specific quantity of CRP fields from grassland to cropland to simulate conversion to crop production. As an example, in our 25% loss scenario, we converted all CRP fields with an assigned random number between 0.00 and 0.25 to cropland. Thus, in our data layer creation we followed the assumption that if a farmer decided to remove land from a conservation program, this decision would be made at a field-by-field level, i.e., the farmer would not remove just a portion of a field from the program. In our 100% loss scenario, we also assumed that all CRP grasslands would be returned to crop production. While some CRP grasslands would undoubtedly remain in perennial cover after contract expiration, conversion of other, non-CRP, grasslands to croplands in the region would likely more than compensate for this disparity. Following these procedures and assumptions, we created land-cover layers representing 0%, 10%, 25%, 50%, 75%, and 100% loss of CRP grasslands. We compared land-cover layers for each percentage loss scenario to total CRP grassland area in the 0% loss layer to verify that the correct percentage of CRP grassland was converted to cropland.

In InVEST, habitats are influenced by their distance from potential threats and their susceptibility to those threats. We developed GIS layers identifying specific threats to amphibian habitat in the PPR. These threat layers were created through a reclassification process of land-cover layers using ArcGIS. We developed four threat layers that included (1) cropland areas, (2) long hydroperiods, i.e., lakes and wetlands identified in NWI as having permanent water regimes, (3) short hydroperiods, i.e., wetlands identified in NWI as having temporary water regimes, and (4) isolation, i.e., wetlands greater than 0.5-km from another wetland. We considered croplands to be a threat to amphibian habitat quality due to the combined effects of increased sedimentation rates, potential for pesticide contamination, and physical alteration of the upland plant and insect communities. NWI identifies water regimes for PPR palustrine wetlands that include, temporary, seasonal, semipermanent, and permanent (Cowardin et al., 1979). We identified a temporary water regime as a threat because wetlands with this water regime often do not contain water over a temporal period long enough for most larval amphibians to survive to metamorphosis. We identified a permanent water regime as a threat due to the predatory fish communities often harbored in wetlands with this water regime. By incorporating water regimes in this way, wetlands with intermediate hydroperiods, i.e., seasonal and semipermanent wetlands, would receive higher quality ratings than wetlands with either very short (temporary) or very long (permanent) hydroperiods. Lastly, we identified isolation as a threat due to the need of some amphibians to use multiple habitat types in an interconnected landscape (i.e., landscape complementation; Pope et al., 2000). We used a 0.5-km separation distance to identify "isolated wetlands" based on an average intrapopulation migration distance (i.e., <1.0 km) as identified by Semlitsch (2008). While there are other threats to amphibian habitat quality, the four we identified encompass the major threats affecting amphibian habitats in the PPR (Mushet et al., 2012a).

We considered that cropland threats could affect amphibian habitats up to a maximum distance of 1-km. All other threats were primarily restricted to within the wetland itself but also influenced habitat across a short (0.1-km) distance of the adjacent buffer. We allowed the strength of threats to decay linearly to zero over the 1-km or 0.1-km distance of influence assigned to specific threat types. A complete description of our development of GIS land-cover and threat layers used in InVEST runs is provided in online Appendix A.

Once land-cover/habitat and threats layers were developed, we used InVEST to quantify amphibian habitat quality and quantity across years of interest (2007–2012) and among our various scenarios of CRP loss (0–100% loss). In the InVEST model, we used an output cell size of 50 m and a half-saturation constant of 70, selected as described in Tallis et al. (2011). In each run (i.e., year or scenario), the model worked to erode the quality value of identified amphibian habitats (initial value = 1) based on spatial proximity to a threat, susceptibility to that threat, and the threat's strength (i.e., threat weight). Output data layers from the model were then used to create maps depicting changes in amphibian habitat quality across years and among scenarios of CRP loss. Quality rating ranges from zero (no value to amphibians) to one (greatest value to amphibians). From our habitat quality maps, we produced summary tables quantifying changes in optimal amphibian habitat quantity (ha) by ecoregions. For these tabulations, we defined optimal amphibian habitat as areas with a habitat rating $\geqslant$0.8. Our completed InVEST susceptibility and threat tables, including habitat designations, threat weights, decay functions, and susceptibility values, are provided in online Appendix B. Lastly, we varied values used as thresholds and in susceptibility and threat tables individually over a range of values to explore the sensitivity of our results to values used, thereby providing an indication of the robustness of model results (online Appendix C).

3. Results

From 2007 to 2012, actual amount of CRP lands in the four states containing much of the PPR declined from more than 3.5 million ha to just over 2.3 million ha, a 35% decline (Table 1). The largest losses (−47%) occurred in the state of North Dakota where CRP lands declined from approximately 1.4 million ha in 2007 to just over 730,000 ha in 2012. Iowa suffered the smallest losses, but still lost greater than 20% of its CRP lands. Our modeling results show that over the same 2007–2012 period, optimal amphibian habitat in the four ecoregions we modeled declined by approximately 22%, from a high of 3.8 million ha in 2007 to a low of 2.9 million ha in 2012 (Table 2, and Fig. 2). The Northern and Northwestern Glaciated Plains accounted for over 80% of the optimal amphibian habitat available among the four ecoregions studied. The Des Moines Lobe ecoregion supported little optimal amphibian habitat compared to the other three ecoregions; however, it also showed the lowest percent loss (−3.6%) over our six-year study period. While the amount of CRP on the PPR landscape steadily declined from 2007 to 2012, changes in the availability of optimal amphibian habitat (Table 2) did not always track CRP losses (Fig. 3); for example, optimal amphibian habitat in the Northern Glaciated Plains ecoregion declined by approximately 156,000 ha between 2007 and 2008. However, optimal amphibian habitat in the same ecoregion increased by over 100,000 ha between 2009 and 2011, a period when the amount of CRP lands continued to decline. Additionally, between 2011 and 2012 the Northern Glaciated Plains showed a marked decline in optimal amphibian habitat (−28%) that was out of proportion with CRP losses between these two years. Optimal amphibian habitat in the Northwestern Glaciated Plains and the Lake Agassiz Plain ecoregions also showed similar increases or remained fairly stable over the 2009–2011 period, with sharp declines in 2012.

Our scenario based modeling revealed a marked decline in optimal amphibian habitat (−9% across the PPR) if 25% of current (2012) CRP lands are returned to agricultural production (Table 3). This loss of optimal habitat increases to 26% (a loss of approximately 0.8 million ha) if all CRP lands within the PPR are returned to agricultural production. Our modeling also reveals that the Northern Glaciated Plains would have the greatest loss of optimal amphibian habitat (−32% in our scenario in which all CRP grasslands are converted to cropland (Table 3)). The Des Moines Lobe ecoregion had the smallest amount of amphibian habitat tied to CRP grasslands (17,679 ha), but this represents 20% of the optimal habitat available to amphibians in this ecoregion where amphibian habitat is already extremely rare (Fig. 2).

Results of our sensitivity analyses (online Appendix C) revealed that threshold values used to define optimal amphibian habitat had a significant influence on the amount of habitat so designated. As an example, if a cutoff value of $\geqslant$0.5 was used rather than the $\geqslant$0.8 used in our final model, 2012 optimal amphibian habitat

Table 2
Optimal amphibian habitat (ha) within Northern Glaciated Plains (NGP), Northwestern Glaciated Plains (NWGP), Lake Agassiz Plain (LAP), and Des Moines Lobe (DML) ecoregions of the United States. Optimal amphibian habitat was quantified using the Biodiversity Module of InVEST (Natural Capital Project, 2013) modeling suite.

State	2007	2008	2009	2010	2011	2012	Change 2007–2012	% Change 2007–2012
NGP	1,453,025	1,297,078	1,409,038	1,585,585	1,521,861	1,103,083	−349,942	−24
NWGP	1,675,353	1,551,451	1,452,266	1,473,106	1,461,618	1,300,099	−375,254	−22
LAP	565,202	503,504	489,838	495,409	483,241	451,185	−114,017	−20
DML	90,907	81,115	82,914	69,907	77,980	87,660	−3,247	−3.6
Total	3,784,486	3,433,146	3,434,056	3,624,006	3,544,700	2,942,026	−842,460	−22

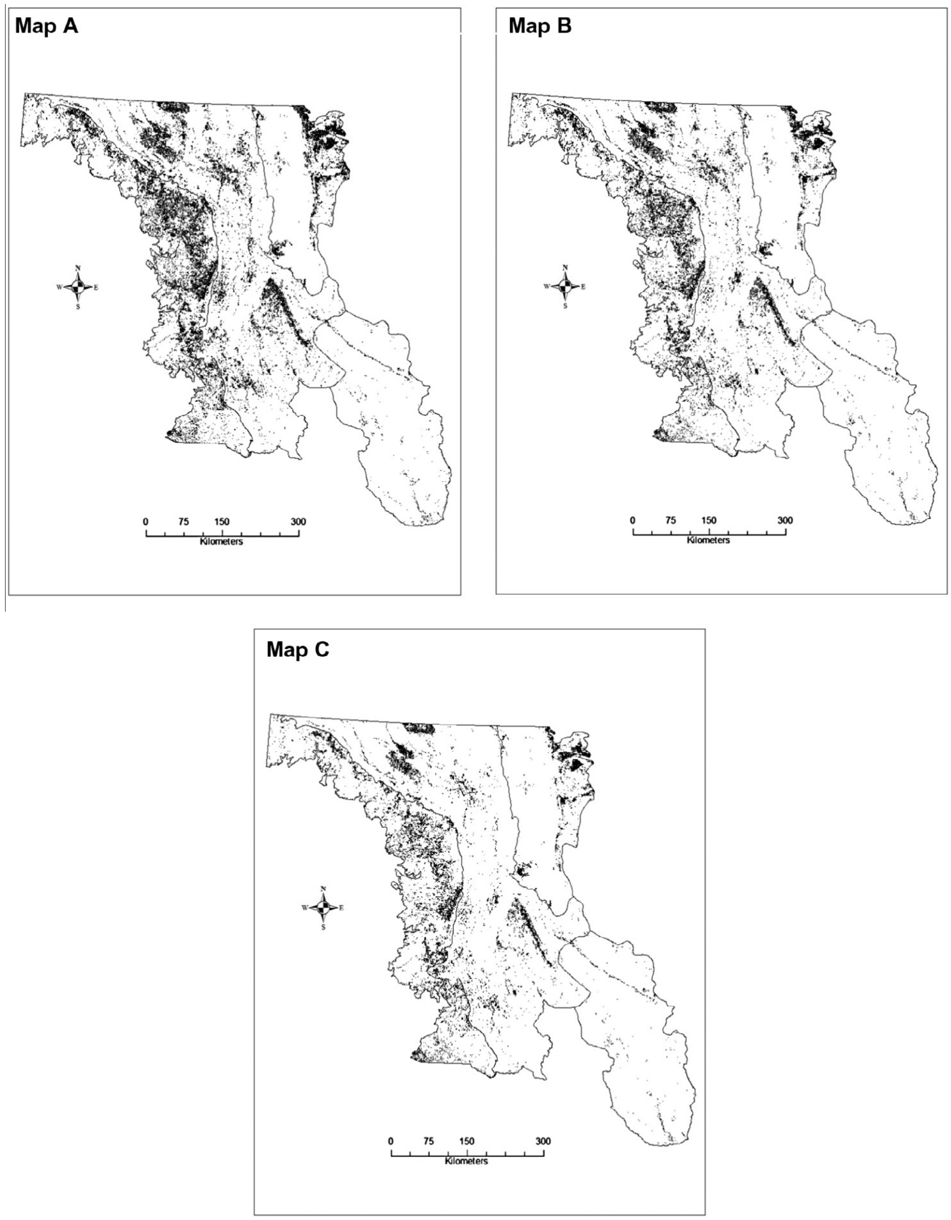

Fig. 2. Distribution of optimal amphibian habitat (indicated in black) in the Prairie Pothole Region of the United States in 2007 (Map A), 2012 (Map B), and under a scenario in which all Conservation Reserve Program (CRP) grasslands present in 2012 are converted to crop production (Map C).

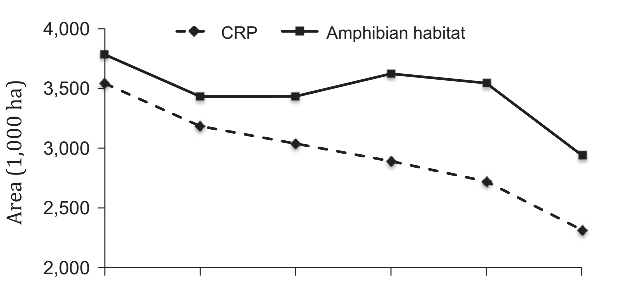

Fig. 3. Optimal amphibian habitat and area of Conservation Reserve Program (CRP) lands in the Prairie Pothole Region of the North Dakota, South Dakota, Minnesota, and Iowa, 2007–2012.

estimates for the Northern Glaciated Plains ecoregion increased from 1,103,083 ha to 1,727,126 ha. Thus, our results using a 0.8 cutoff value should be considered as conservative estimates. However, even using a 0.5 threshold value, area identified as optimal amphibian habitat in this ecoregion still declined by approximately 20.6% between 2007 and 2012 (online Appendix C). As expected, effect distance and weight assigned to crop threats also had a significant influence on results (online Appendix C). However, these effects are consistent with the level of alteration associated with the conversion of grassland cover types to croplands in the PPR and known effects of habitat alterations to amphibian occurrence (e.g., Balas et al. 2012; Mushet et al. 2012a,b).

4. Discussion

Our use of InVEST revealed that the loss of optimal amphibian habitat in the PPR of the United States has been significant. Additionally, these losses will continue if additional CRP lands are converted to crop production. In our scenario in which all-remaining CRP lands are returned to crop production, losses of amphibian

Table 3
Area (ha) of optimal amphibian habitat in the Northern Glaciated Plains (NGP), Northwestern Glaciated Plains (NWGP), Lake Agassiz Plain (LAP), and Des Moines Lobe (DML) ecoregions of the United States under various scenarios reflecting the conversion of 10%, 25%, 50%, 75%, and 100% of Conservation Reserve Program (CRP) grasslands to croplands. Optimal amphibian habitat was quantified using the Biodiversity Module of InVEST (Natural Capital Project, 2013) modeling suite. Values in parentheses represent the percentage of current (2012) optimal amphibian habitat lost under various levels of CRP loss.

Scenario	NGP	NWGP	LAP	DML	Total
Current (2012)	1,103,083	1,300,099	451,185	87,660	2,942,027
−10% CRP	1,053,012 (−5%)	1,265,095 (−3%)	436,341 (−3%)	85,222 (−3%)	2,839,678 (−3%)
−25% CRP	974,321 (−12%)	1,216,499 (−6%)	414,887 (−8%)	81,075 (−8%)	2,686,780 (−9%)
−50% CRP	870,837 (−21%)	1,136,345 (−13%)	383,126 (−15%)	77,448 (−12%)	2,467,756 (−16%)
−75% CRP	800,287 (−27%)	1,076,976 (−17%)	360,605 (−20%)	73,143 (−17%)	2,311,011 (−21%)
−100% CRP	750,997 (−32%)	1,030,128 (−21%)	339,250 (−25%)	69,981 (−20%)	2,190,356 (−26%)

habitat would equal approximately 26% of the total optimal habitat available across the PPR in 2012. While largely unknown, the effects on amphibians of losing over one-quarter of their remaining optimal habitat would likely be significant. In addition to effects on biodiversity, habitat losses of this magnitude would likely have a negative influence on other ecological attributes (e.g., reproduction, survival, dispersal, recolonization) identified by Mushet et al. (2012a) as being important to the maintenance and viability of amphibian populations and biodiversity.

While losses of CRP lands across the PPR landscape have been significant (Table 1; USDA, 2013), resulting effects on amphibian habitat can be masked by fluctuating climate cycles. During the period 2009–2011, precipitation in many parts of the PPR was above normal. This was especially true in North Dakota where runoff during springtime snowmelt caused flooding and often prevented farmers from getting into their fields to plant crops. This inability of farmers to work their fields is reflected in "Prevented Planting" statistics collected by the USDA. Prevented Planting is a federally subsidized crop insurance program that provides payments to participants when extreme weather conditions prevent expected plantings. In North Dakota alone, Prevented Planting payments were made on 2.2 million ha of croplands that went unplanted in 2011 (Table 4), primarily as a result of springtime flooding. While less than in 2011, in 2009 and 2010, total area where planting was prevented was approximately an order of magnitude greater than in 2007 and 2008. These vast areas of North Dakota that went unplanted in 2009, 2010, and 2011 were typically adjacent to wetland areas (i.e., where fields are most prone to flooding). As a result, our model results suggest that prevented planting areas provided an abundance of habitat for amphibians; habitat that masked losses of optimal habitat resulting from the conversion of CRP lands to croplands. Drier conditions returned to the PPR in 2012, and sharp drops in optimal amphibian habitat (Fig. 3) occurred as a consequence of not only the additional losses of CRP grasslands that occurred between 2011 and 2012, but also due to the loss of habitat that occurred as previously flooded croplands areas were returned to production (Table 4).

The Des Moines Lobe ecoregion provided little optimal amphibian habitat compared to the Northern and Northwestern Glaciated Plains. Thus, conservation grasslands within the Des Moines Lobe region may play an even larger role in terms of amphibian habitat provisioning in this region of habitat scarcity. Our modeling identified only 87,660 ha of optimal amphibian habitat in the Des Moines Lobe. Of this habitat, approximately 20% was provided by CRP lands. In an area where habitat is already extremely scarce, the loss of any amount, let alone the loss of the greater than 17,500 ha currently being provided by CRP, could be devastating. Even with these conservation lands intact, several amphibian species in the region are in decline (e.g., Blanchards cricket frog [*Acris blanchardi*], northern leopard frog [*Lithobates pipiens*]; Lannoo et al., 1994; Hemesath, 1998). While large, our amphibian habitat loss estimates for the Des Moines Lobe ecoregion are likely conservative as 2012 was a wet year in this southern most ecoregion of the PPR. As with the Northern and Northwestern Glaciated Plains ecoregions from 2009 to 2011, some optimal habitat losses due to declines in conservation lands could be masked by habitat created during the wet conditions. Additionally, while CRP lands have been in decline, other conservation programs have contributed to amphibian habitat availability in recent years. As an example, over 1900 ha of wetlands and adjacent upland habitat has been created in Iowa as part of the USDA Natural Resources Conservation Service's Wetlands Reserve Program (WRP). This habitat is under long-term easement agreements and not as vulnerable to loss as conservation lands protected solely by short-term contracts (e.g., CRP).

Much like the Des Moines Lobe, the Lake Agassiz Plain ecoregion has lost most of its natural wetland and grassland habitat due to intensive agricultural development. Of the 451,185 ha of optimal amphibian habitat identified in the Lake Agassiz Plain, over 110,000 ha (approximately 25%) is available as a direct result of CRP grasslands. Again, how loss of this habitat would ultimately affect the region's amphibians is largely unknown. However, we can be certain that the trajectory of the effect would not be positive.

The Northern and Northwestern Glaciated Plains each had significantly more optimal amphibian habitat than the other ecoregions we modeled. However, of the two, availability of optimal habitat was more dependent on CRP lands in the Northern Glaciated Plains than in the Northwestern Glaciated Plains. Most of the Northwestern Glaciated Plains is made up of an area known as the Missouri Coteau. The topography of the Missouri Coteau is varied with greater local relief and rockier, less fertile, soils than in the Northern Glaciated Plains to the east. As a result, croplands, while still the major land-use, are less abundant and native grassland pastures and rangelands form a larger component of the Northwestern Glaciated Plains landscape. These pastures and rangelands provide the grassland habitat component used by amphibians and serve to buffer aquatic habitats from the effects of crop production in adjacent uplands. While CRP still provides significant areas of amphibian habitat in the Northwestern Glaciated Plains, other areas of grassland habitats also contribute towards the maintenance of the region's amphibian biodiversity. In the Northern Glaciated Plains where these alternate grasslands are not as abundant, habitat components provided by CRP grasslands become a more important amphibian habitat component

Table 4
Area (ha) of croplands in North Dakota that were classified as not planted in a given year, 2007–2012 (USDA Farm Service Agency Annual Acreage Reporting Summaries – North Dakota).

Year	Prevented planting (ha)
2007	90,420
2008	12,252
2009	793,529
2010	698,588
2011	2,274,832
2012	65,888

on the landscape (i.e., providing approximately 32% of the optimal habitat available to amphibians).

The results of our modeling efforts identify recent past and potential future amphibian habitat losses in the PPR of the United States. However, they also identify opportunities for the improvement of amphibian habitats if current trends can be reversed, either through gains in CRP or through other conservation programs that lead to increases in grassland and wetland habitats on the PPR landscape (e.g., USDA Natural Resources Conservation Service's Wetlands Reserve Program [WRP] and Grasslands Reserve Program [GRP]). The potential of conservation grasslands to mitigate amphibian habitat loss in the PPR has been demonstrated by the amount of optimal habitat that has been created on the landscape through a single conservation program, CRP. If CRP was not as successful as it has been in providing amphibian habitat on the PPR landscape, we would not see losses of these lands from the landscape resulting in such significant declines in optimal amphibian habitat in our modeled scenarios. Thus, CRP and other conservation programs can play a significant role in restoring amphibian habitats in the PPR. However, care must be taken to recognize the transitory nature of conservation lands that are not protected through fee-title ownership or through long-term easements. As seen through recent losses of CRP lands across the PPR landscape, lands protected through short-term contracts will likely revert to other uses during periods when conservation payments lag behind profits that can be realized through conversion to other uses.

Economic climates favoring commodity production over conservation has resulted, and will likely continue to result, in a loss of amphibian habitat not just in the PPR, but worldwide. The resulting impact on amphibians dependent upon habitat provided by conservation lands could be substantial. This is especially troubling when considering that one-third of the world's known amphibian species are already at high risk of extinction (Norris, 2007). However, reversing recent trends in grassland losses through the implementation of additional conservation practices providing perennial grassland cover on agricultural lands has great potential to mitigate for habitat losses through the creation of alternate habitats. Our results are applicable beyond the PPR in areas where amphibian habitats consist of wetlands imbedded in a grassland matrix and economic pressures favor the conversion of natural and/or conservation grasslands to cropland. By quantifying amphibian habitat through use of scenarios-based models such as InVEST, insights into potential effects of land-cover change can be obtained thereby facilitating conservation and mitigation efforts.

Acknowledgments

Financial support for this effort came from the United States Department of Agriculture's Natural Resources Conservation Service (NRCS) through their Conservation Effects Assessment Project (CEAP—Wetlands) and the Farm Service Agency (FSA) Economics and Policy Analysis Staff. We thank our partners in NRCS and FSA for their financial support. Additionally, we thank Scott McMurry and four anonymous reviewers for their critical reviews of earlier drafts of our manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendices. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.04.001.

References

Adams, M.J., Miller, D.A., Muths, E., Corn, P.S., Campbell Grant, E.H., Bailey, L.L., Fellers, G.M., Fisher, R.N., Sadinski, W.J., Waddle, H., Walls, S.C., 2013. Trends in amphibian occupancy in the United States. PLoS ONE 8 (5), e64347. http://dx.doi.org/10.1371/jpurnal.pone.0064347.

Balas, C.J., Euliss Jr., N.H., Mushet, D.M., 2012. Influence of conservation programs on amphibians using seasonal wetlands in the prairie pothole region. Wetlands 32, 333–345.

Batt, B.D., Anderson, M.G., Anderson, C.D., Caswell, F.D., 1989. The use of prairie potholes by North American ducks. In: van der Valk, A. (Ed.), Northern prairie wetlands. Iowa State University Press, Ames, pp. 204–227.

Chanson, J.S., Hoffmann, M., Cox, N.A., Stuart, S.N., 2008. The State of the World's Amphibians. In: Stuart, S.N., Hoffman, M., Chanson, J.S., Cox, N.A., Berridge, R.J., Ramani, P., Young, B.E. (Eds.), *Threatened Amphibians of the World*, Lynx Edicions, Barcelona; IUCN, Gland; and Conservation International, Arlington, pp. 33–52.

Classen, R., Carriazo, F., Cooper, J.C., Hellerstein, D., Ueda, K., 2011. Grassland to cropland conversion in the Northern Plains: the role of crop insurance, commodity, and disaster programs. US Department of Agriculture, Economic Research Service, Washington.

Cowardin, L.M., Carter, V., Golet, F.C., LaRoe, E.T., 1979. Classification of wetlands and deepwater habitats of the United States, FWS/OBS-79/31, US Fish and Wildlife Service; Washington.

Cox, N.A., Berridge, R.J., Church, D., Paul van Dijk, P., Kusrini, M., Lau, M., Oldfield, T., Rollins-Smith, L., Xie, F., 2008. Why save amphibians. In: Stuart, S.N., Hoffman, M., Chanson, J.S., Cox, N.A., Berridge, R.J., Ramani, P., Young, B.E. (Eds.), Threatened Amphibians of the World, Lynx Edicions, Barcelona; IUCN, Gland; and Conservation International, Arlington, pp. 23–29.

Dahl, T.E., 1990. Wetlands losses in the United States 1780's to 1980's. US Department of the Interior, Fish and Wildlife Service; Washington.

Davic, R.D., Welsh Jr., H.H., 2004. On the ecological roles of salamanders. Annu. Rev. Ecol. Syst. 35, 405–434.

Environment Canada, 1986. Wetlands in Canada: a valuable resource, Fact Sheet 86–4, Lands Directorate, Ottawa.

Euliss Jr., N.H., Smith, L.M., Liu, S., Feng, M., Mushet, D.M., Auch, R.F., Loveland, T.R., 2010. The need for simultaneous evaluation of ecosystem services and land-use change. Environ. Sci. Technol. 44, 7761–7763.

Euliss Jr, N.H., Wrubleski, D.A., Mushet, D.M., 1999. Wetlands of the prairie pothole region: invertebrate species composition, ecology, and management. In: Batzer, D.P., Rader, R.B., Wissinger, S.A. (Eds.), Invertebrates in Freshwater Wetlands of North America: Ecology and Management. John Wiley and Sons, New York, pp. 471–514.

Fritzell, E.K., 1989. Mammals in prairie wetlands. In: van der Valk, A.G. (Ed.), Northern Prairie Wetlands. Iowa State University Press, Ames, pp. 268–301.

Harper, E.B., Rittenhouse, T.A.G., Semlitsch, R.D., 2008. Demographic consequences of terrestrial habitat loss for pool-breeding amphibians: predicting extinction rates associated with inadequate size of buffer zones. Conserv. Biol. 22, 1205–1215.

Hemesath, L.M., 1998. Iowa's frog and toad survey, 1991–1994. In: Lannoo, M.J. (Ed.), Status & Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, pp. 206–216.

Higgins, K.F., Naugle, D.E., Forman, J.R., 2002. A case study of changing land use practices in the northern Great Plains, U.S.A.: an uncertain future for waterbird conservation. Waterbirds 25 (Special Publication 2), 42–50.

Igl, L.D., Johnson, D.H., 1998. Wetland birds in the northern Great Plains. In: Mac, M.J., Opler, P.A., Puckett Haecker, C.E., Doran, P.D. (Eds.), *Status and Trends of the Nation's Biological Resources*, vol. 2, US Department of the Interior, US Geological Survey; Reston, pp. 454–455.

Kantrud, H.A., Krapu, G.L., Swanson, G.A., 1989. Prairie basin wetlands of the Dakotas: A community profile, US Fish and Wildlife Service, Biol Rep, 85(7.28).

Lannoo, M.J., Lang, K., Waltz, T., Phillips, G.S., 1994. An altered amphibian assemblage: Dickinson County, Iowa, 70 years after Frank Blanchard's survey. Am. Midl. Natl. 131, 311–319.

Lannoo, M.J., 2012. A perspective on amphibian conservation in the United States. Alytes 29, 133–144.

Larson, D.L., Euliss Jr., N.H., Lannoo, M.J., Mushet, D.M., 1998. Amphibians of northern grasslands. In: Mac, M.J., Opler, P.A., Puckett Haecker, C.E., Doran, P.D. (Eds.), Status and Trends of the Nation's Biological Resources, vol. 2, US Department of the Interior, US Geological Survey, Reston, 450–451.

Leitch, J.A., 1989. Politicoeconomic overview of prairie potholes. In: Van der Valk, A.G. (Ed.), Northern Prairie Wetlands. Iowa State University Press, Ames, pp. 2–15.

McCallum, M.L., 2007. Amphibian decline or extinction? Current declines dwarf background extinction rates. J. Herpetol. 41, 483–491.

Merrell, D.J., 1970. Migration and gene dispersal in *Rana pipiens*. Am. Zool. 10, 47–52.

Millenium Ecosystem Assessment, 2003. Ecosystems and human well-being: a framework for assessment. Millenium Ecosystem Assessment, Washington.

Mushet, D.M., Euliss Jr., N.H., Stockwell, C.A., 2012a. A conceptual model to facilitate amphibian conservation in the northern Great Plains. Gt. Plains Res. 22, 45–58.

Mushet, D.M., Euliss Jr., N.H., Stockwell, C.A., 2012b. Mapping anuran habitat suitability to estimate effects of grassland and wetland conservation programs. Copeia 2012, 322–331.

Natural Capital Project, 2013. InVEST Version 2.4.5, <http://www.naturalcapitalproject.org/download.html>. accessed 04.03.13.

Nelson, E., Cameron, D.R., Regetz, J., Polasky, S., Daily, G.C., 2011. Terrestrial biodiversity. In: Kareiva, P., Tallis, H., Ricketts, Daily GC, Polasky S, T.H., Daily, G.C., Polasky, S. (Eds.), Natural capital: theory and practice of mapping ecosystem services. Oxford University Press, Oxford, pp. 229–245.
Northern Great Plains Floristic Quality Assessment Panel, 2001. Coefficients of conservatism for the vascular flora of the Dakotas and adjacent grasslands, US Geological Survey, Inform Tech Rep, USGS/BRD/ITR-2001-0001.
Norris, S., 2007. Ghosts in our midst: coming to terms with amphibian extinctions. Biosci 57, 311–316.
O'Rourke, D.P., 2007. Amphibians used in research and teaching. ILAR J. 48, 183–187.
Pough, F.H., 1980. The advantages of ectothermy for tetrapods. Am. Nat. 115, 92–112.
Pope, S.E., Fahrig, L., Merriam, H.G., 2000. Landscape complementation and metapopulation effects on leopard frog populations. Ecol 81, 2498–2508.
Rashford, B.S., Walker, J.A., Bastian, C.T., 2011. Economics of grassland conversion to cropland in the Prairie Pothole Region. Cons. Biol. 25, 276–284.
Regan, H.M., Lupia, R., Drinnan, A.N., Burgman, M.A., 2001. The currency and tempo of extinction. Am. Nat. 157, 1–10.
Regester, K.J., Lips, K.R., Whiles, M.R., 2006. Energy flow and subsides associated with the complex life cycle of ambystomatid salamanders in ponds and adjacent forest in Illinois. Oecologia 147, 303–314.
Seale, D.B., 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. Ecol 61, 1531–1550.
Semlitsch, R.D., 2000. Principles of management for aquatic breeding amphibians. J. Wild. Manage. 64, 615–631.
Semlitsch, R.D., 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. J. Wild. Manage. 72, 260–267.
Semlitsch, R.D., Bodie, J.R., 2003. Biligical criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conserv. Biol. 17, 1219–1228.
Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W., 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306, 1783–1785.
Swengel, A.B., Swengel, S.R., 1998. Tall-grass prairie butterflies and birds. In: Mac, M.J., Opler, P.A., Puckett Haecker, C.E., Doran, P.D. (Eds.), *Status and Trends of the Nation's Biological Resources*, vol. 2, US Department of the Interior, US Geological Survey, Reston, pp. 446–447.
Tallis, H.T., Ricketts, T., Guerry, A.D., Wood, S.A., Sharp, R., Nelson, E., Ennaanay, D., Wolny, S., Olwero, N., Vigerstol, K., Pennington, D., Mendoza, G., Aukema, J., Foster, J., Forrest, J., Cameron, D., Arkema, K., Lonsdorf, E., Kennedy, C., Verutes, G., Kim, C.K., Guannel, G., Papenfus, M., Toft, J., Marsik, M., Bernhardt, J., 2011. InVEST 2.4.5 User's Guide. The Natural Capital Project, Stanford.
US Department of Agriculture, 2013. CRP Contract Summary and Statistics: Annual Summary, <http://www.fsa.usda.gov/FSA/webapp?area=home&subject=copr&topic=crp-st> (accessed 13.11.13).
US Environmental Protection Agency, 2013. Level III and IV ecoregions of the continental United States, <http://www.epa.gov/wed/pages/ecoregions/level_iii_iv.htm>. accessed 04.03.13.
Vanni, M.J., 2002. Nutrient cycling by animals in freshwater ecosystems. Annu. Rev. Ecol. Syst. 33, 341–370.
Wright, C.K., Wimberly, M.C., 2013. Recent land use change in the Western Corn Belt threatens grasslands and wetlands. Proc. Natl. Acad. Sci. 110, 4134–4139.